SEXUAL DIMORPHISM IN MID-CRETACEOUS HEMIASTERID ECHINOIDS

by DIDIER NÉRAUDEAU

ABSTRACT. Fossil hemiasterid echinoids of *Hemiaster* (*Leymeriaster*) are sexually dimorphic, females having wider gonopores than males. No other conspicuous morphological differences permit the two sexes to be distinguished, but in certain populations females achieve larger sizes than males and consequently seem hypermorphic.

SEXUAL dimorphism, common in modern echinoids, in many cases affects only gonopore size (Smith 1984) with specimens considered to be female having wider genital pores (e.g. David *et al.* 1988). However, a few species living in cold or deep waters show more spectacular types of sexual dimorphism, a commoner one being the presence of marsupia on the female test (Pearse and McClintock 1990; Schatt and Féral 1991). Another type of morphological sexual dimorphism, recently discovered by David and Mooi (1990), is the presence of internal brooding pouches in the female test of Antarctic urechinid echinoids.

Of these different types of sexual dimorphism, only the last is still unknown in fossil species. Indeed, the size of genital pores has been described as a sexually dimorphic character for several fossil clypeasteroids (Kier 1967, 1968, 1969) and for a few cassiduloids (Philip 1963; Kadil'nikova and Moskvin 1984). Moreover, Kier (1969) and Philip and Foster (1971) have reported the presence of marsupia in fifteen Cretaceous and eleven Cenozoic species, including arbacioids, clypeasteroids, spatangoids and one phymosomatoid.

Apart from the Maastrichtian spatangoid *Cyclaster platornatus* from Belgium (Jagt and Michels 1990), which are as sexually dimorphic as the Tertiary species of *Cyclaster* (Henderson 1975), almost all dimorphic Cretaceous echinoids are regular species (Kier 1969). So, until now, only allusions to sexual dimorphism have been made by palaeontologists studying Cretaceous hemiasterids (see below). This paper presents the first example of conspicuous sexual dimorphism among these fossil spatangoid echinoids.

PREVIOUS ALLUSIONS TO SEXUAL DIMORPHISM IN FOSSIL HEMIASTERID ECHINOIDS

Lambert (1889) distinguished between North European species of Cretaceous hemiasterids, with petals flush with the test as in *Hemiaster* (*Bolbaster*) *nasutulus*, and North African species, with deep ambulacra excavated like a marsupium as in *Mecaster latigrunda*. However, he used the term 'marsupium' in a descriptive way, never introducing the notion of sexual dimorphism and brooding pouches. Gauthier (1902) defined a morphological variety of *Mecaster noemiae*, named '*gulgulensis*', which was more extended posteriorly than typical specimens, and was also more inflated. Because this variety had fundamental similarities of ambulacra, peristome and periproct with *Mecaster noemiae*, Gauthier supposed that its morphological differences from the typical specimens might be sexual differences. Moreover, Fourtau (1911) described, among other Turonian echinoids from Egypt, two species of *Mecaster*, *M. aly* and *M. humei*, considering the first to be male, and the second female. A few years later, Lambert (1913) noticed the presence of morphologically intermediate specimens and ironically asked if they corresponded to hermaphrodites. Finally,

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Devriès (1960) considered that the petals of *Mecaster fourneli* were sufficiently excavated to act as marsupia, developing the hypothesis introduced by Lambert (1933) for a single small *M. fourneli* with deep ambulacra. None of these authors founded their interpretations on biometric analysis or genital characteristics.

Only Cottreau (1922) has presented a detailed example of morphological dimorphism among fossil hemiasterids, describing dimorphism in *Hemiaster* (*Bolbaster*) *madagascariensis* relating to the shape of the test. The species comprised two morphological groups, one corresponding to individuals with a slightly inclined aboral surface, a non-angular posterior edge between non-divergent petals, and a weakly posterior apical system; the other, with an angular, more inclined test with a short and hard posterior edge, and conspicuously posterior apical system. Cottreau found no morphologically intermediate specimens and thought that differences between the two groups corresponded to a sexual dimorphism. Unfortunately he gave no information about the gonopore size and therefore no genital dimorphism can be associated with these morphological differences.

SEXUAL DIMORPHISM IN CENOMANIAN–TURONIAN HEMIASTERIDS

Material and methods

To test the hypotheses of sexual dimorphism in hemiasterid echinoids, numerous species of these spatangoids have been subjected to biometric analysis. Three examples are selected to illustrate the main results: (1) *Hemiaster* (*Leymeriaster*) *similis* from the Upper Cenomanian of the west coast of France (fifty-five specimens from Port-des-barques, Charente-Maritime, and thirty-three others from Challans-Commequiers, Vendée); (2) *H.* (*L.*) *leymeriei* from the Lower Turonian of west-central France (thirty-seven specimens from Briollay, Anjou); and (3) *Mecaster cenomanensis* from the Lower Cenomanian of Charente-Maritime, west coast of France (seventy-five specimens). For each species, several populations have been biometrically analysed to detect interpopulational and intraspecific differences.

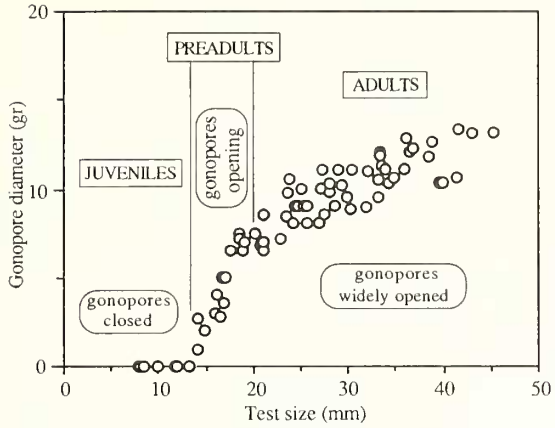
For each species, all the specimens of a single population come from one thin lithological unit of a single outcrop. In order to analyse homologous measurements statistically, the gonopore sizes as a whole correspond to the right posterior genital pore. Its largest diameter was measured with an ocular micrometer. After the distinction of genital dimorphism, several morphological parameters, particularly the shape of test and ambulacra, have been analysed in relation to the gonopore diameter to detect possible secondary sexual differences between males and females.

The material used in this study is housed in Centre des Sciences de la Terre, Université de Dijon (STD).

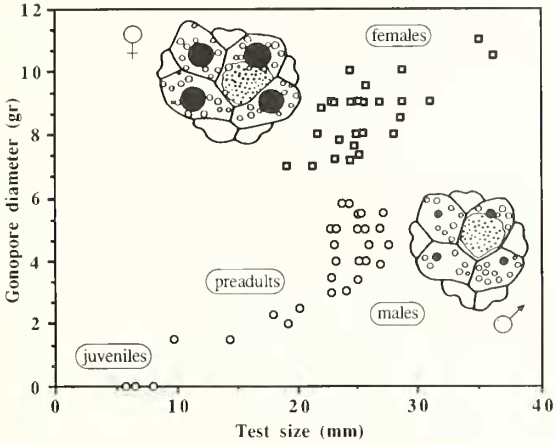
Biometric results and interpretations

Sexual maturity and relative age of fossil hemiasterid echinoids. Previous biometric analyses of gonopore diameter variation in fossil hemiasterid populations (Néraudeau 1990) have shown that it is often easy to distinguish juveniles from adults and to characterize an intermediary stage corresponding to a pre-adult phase of development. Indeed, the ontogeny of fossil hemiasterid echinoids comprises two main morphological crises: the first when the genital pores open, showing the end of the juvenile stage; and the second preceding the acquisition of the final adult morphology and sexual maturity (Text-fig. 1). Between these two crises, associated with two precise size limits, there is a rapid increase in the diameter of the gonopores characterizing the pre-adult stage (David 1980; David and Laurin 1991; Néraudeau 1991).

Growth stages of Hemiaster (L.) similis. The genital pores of *Hemiaster* (*Leymeriaster*) *similis* are generally closed until a test size of 10 mm, sometimes even 12 mm, is reached (Néraudeau and Moreau 1989) (Text-fig. 2). The smallest individuals, without gonopores, can be considered as sexually immature juveniles. These juveniles are always infrequent in fossil populations of adult individuals, being often grouped apart in marly lithofacies, whereas adults abound in chalky ones (Néraudeau 1989).



TEXT-FIG. 1. Sexual maturity and relative age of a fossil hemiasterid echinoid defined by the variations in gonopore diameter (30 gr. = 1 mm). Example given is for the Turonian species *Mecaster verneuili*. Individuals with closed gonopores are juveniles. The rapid opening of gonopores corresponds to a pre-adult stage of development preceding the acquisition of sexual maturity. When the gonopores are widely open, the echinoids are adults and sexually mature.



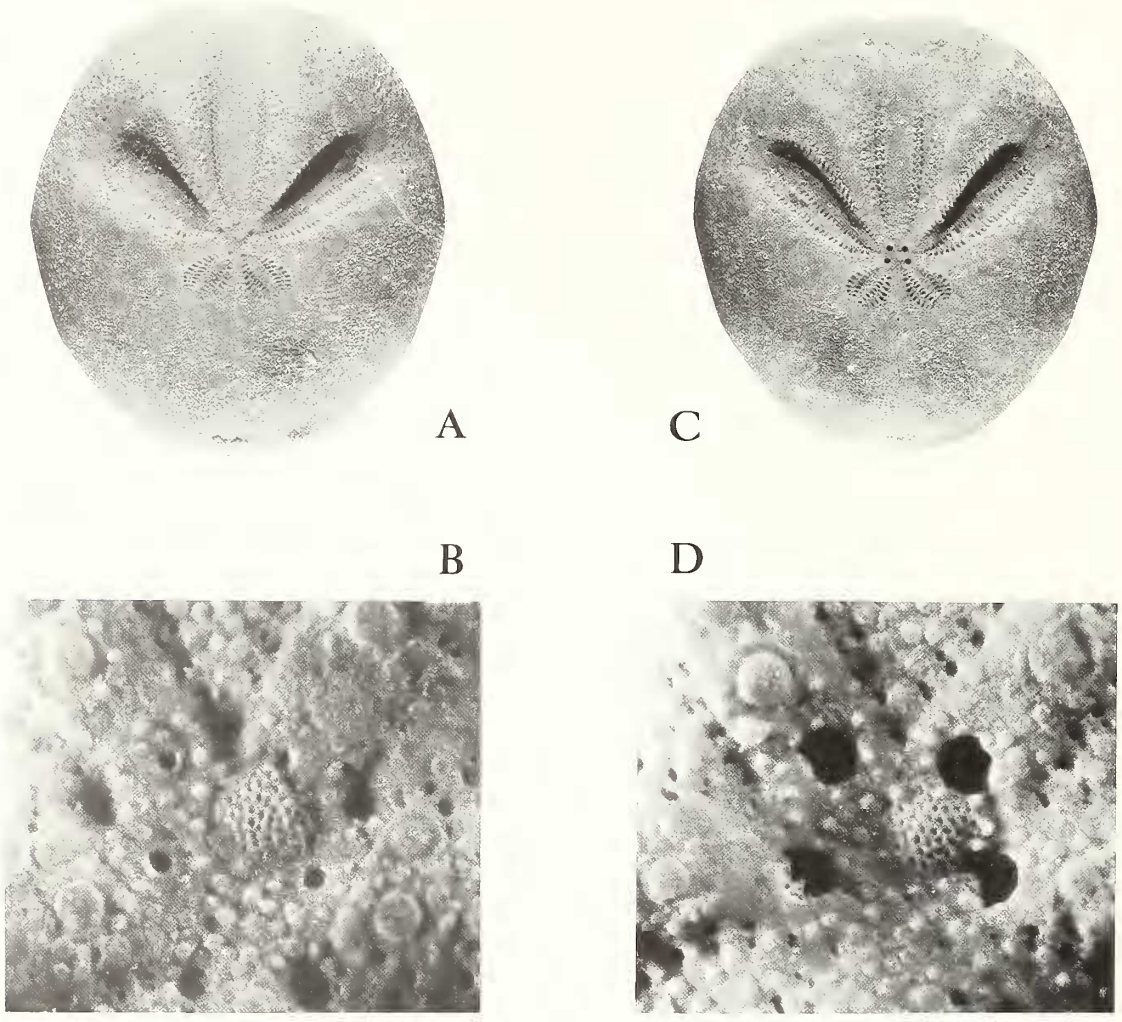
TEXT-FIG. 2. Scatter diagram showing the variations in the diameter of the gonopores (30 gr. = 1 mm) according to the test sizes for *Hemiaster* (*Leymeriaster*) *similis* from the Upper Cenomanian of Port-des-barques, Charente-Maritime. The specimens without genital pores correspond to juveniles. The opening of the gonopores, between 10 and 20 mm, mark the pre-adult stage. Specimens longer than 19–20 mm are adult, sexually mature and dimorphic, the females having gonopores conspicuously wider than the male ones, as indicated on the apical systems illustrated.

After the gonopores open, they rapidly increase in diameter during an ontogenic stage where the test has not achieved all the characteristics of the species morphology. This pre-adult stage of development, like the juvenile stage, is demographically poorly represented in the populations. Finally, the adult-specific morphology is achieved at sizes between 19 and 21 mm, when most of the morphological characters reach relative stability.

Sexual dimorphism in adult Hemiaster (L.) similis. Variations in gonopore diameter distinguish two groups of adult individuals, with wide and small genital pores respectively (Text-fig. 2). In accordance with the recent sea-urchin dimorphism, specimens with large gonopores can be considered to be females (Tahara *et al.* 1960; Kier 1967; David *et al.* 1988). The other specimens, whose gonopore diameter corresponds on average to 55 per cent of that of the female, can be considered to be males.

In this reference population, twenty-five adult individuals can be considered to be females, twenty-two to be males and, therefore, females are slightly more numerous than males with a proportion of fifty-three per cent (in adult specimens only). The result of a binomial probability statistic ($P = 0{\cdot}1$) shows that these ratios deviate significantly from a random sampling of a 50:50 male to female ratio. However, no palaeontological or sedimentological information permits definition of the fossil assemblage as a 'census assemblage' (Cadée 1982; Néraudeau 1991) where the male and female numbers would reflect exactly the sex ratio and the demographic structures of a local echinoid settlement.

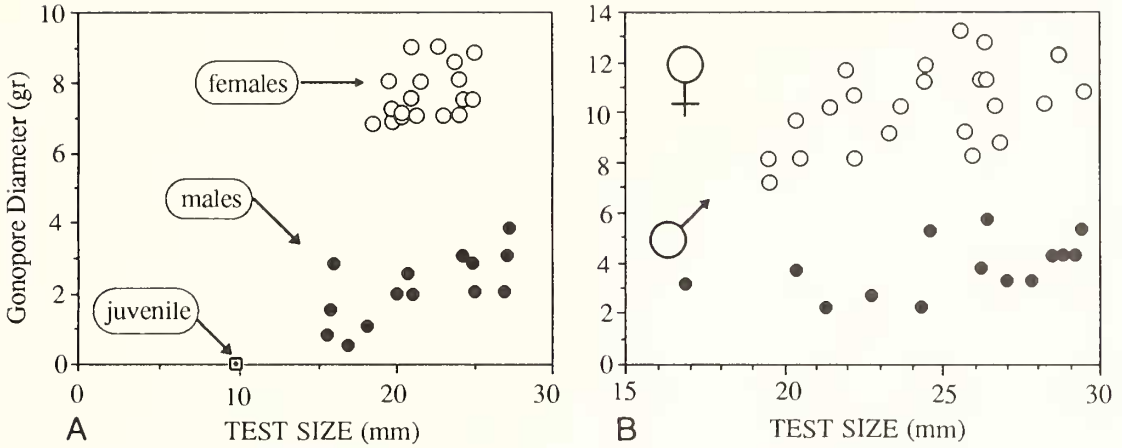
Stratigraphical and geographical variations of the dimorphism. Hemiaster (*L.*) *similis* and closely related species are rather common in the outcrops of Cenomanian to Turonian age in northern Aquitaine and Anjou, France. Different populations, analysed in the same way as the reference population, show a conspicuous genital dimorphism where the females have gonopores two to three times wider than those of the male (Text-fig. 3). Moreover, females are often more numerous than



TEXT-FIG. 3. Male and female of the hemiasterid *Hemiaster* (*Leymeriaster*) *leymeriei* (Agassiz), Lower Turonian of Briollay, Anjou. A, dorsal view of a male specimen (STD B1M), ×2. B, apical system of the same specimen showing the four small gonopores, ×24. C, dorsal view of a female specimen (STD B2F), ×2. D, apical system of the same specimen showing the four wide gonopores, ×24.

males in the populations, the male to female ratios deviating significantly from random sampling of 50:50 male to female ratio, according to binomial probability statistics ($P < 1{\cdot}5$ for the following examples).

Contemporaneous populations of *H.* (*L.*) *similis* show conspicuous sexual dimorphism, whatever their geographical location. For example, for *H.* (*L.*) *similis* from Challans-Commequiers, 200 km

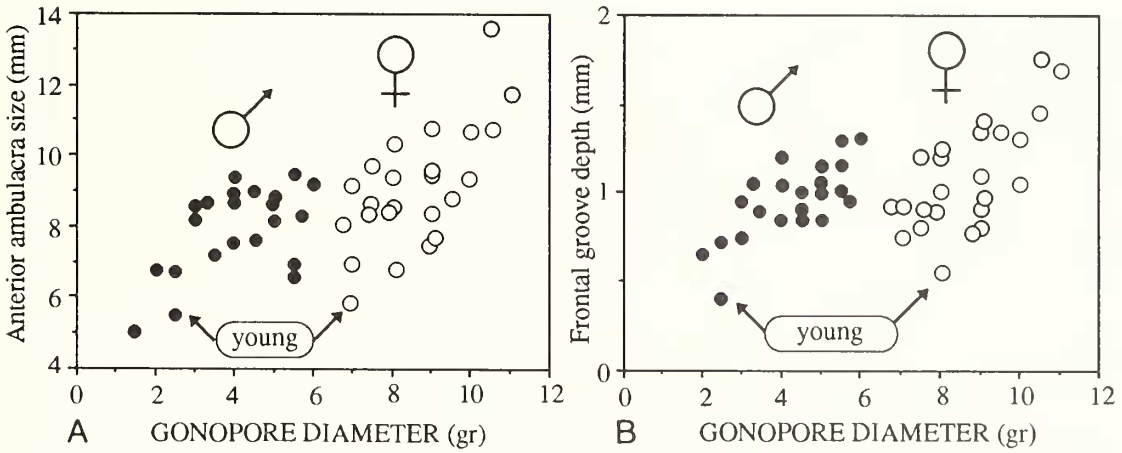


TEXT-FIG. 4. Diagrams showing the variation in gonopore diameter (30 gr. = 1 mm) according to test size in two *Hemiaster* (*Leymeriaster*) populations closely related to the reference population in Text-fig. 2. A, *H.* (*L.*) *similis* from Challans-Commequiers, contemporaneous with the reference population but geographically distant. B, *H.* (*L.*) *leymeriei* from Briollay, Anjou, a Turonian descendant of *H.* (*L.*) *similis*.

to the north of the reference population, adult individuals comprise eighteen females (56 per cent) and fourteen males (44 per cent) in the sample studied (Text-fig. 4A).

Moreover, compared to the Cenomanian species *H.* (*L.*) *similis*, the dimorphism of its Turonian descendant *H.* (*L.*) *leymeriei* seems conspicuously expressed too. Males of *H.* (*L.*) *leymeriei* have gonopores whose diameter corresponds on average to 34 per cent of that of the female (Text-fig. 4B). In the sample studied, twenty-two specimens from the thirty-seven adult individuals collected are females (62 per cent) and only fourteen of them are males (38 per cent).

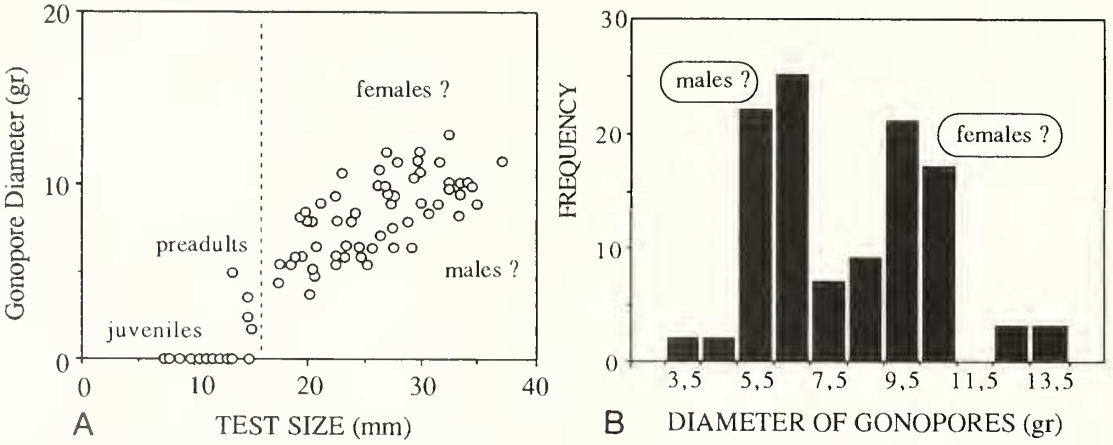
Research of secondary sexual differences. Exhaustive biometric analyses of *H.* (*L.*) *similis* and *H.* (*L.*) *leymeriei* (Néraudeau 1990) reveal that the two sexes of these species present no real morphological differences associated with the genital dimorphism. But in several populations, such as the reference



TEXT-FIG. 5. Scatter diagrams showing the variation in depth of the frontal groove (A) and the variation in size of the anterior ambulacra (B) in the reference population of *Hemiaster* (*Leymeriaster*) *similis* from the Upper Cenomanian of Port-des-barques, Charente-Maritime.

population of *H.* (*L.*) *similis*, the females achieve a larger size than males and consequently show more excavated ambulacra, particularly the anterior pair and the frontal groove (Text-fig. 5A). The anterior petals of the females are, in these cases, more extended than those of the males, both in depth and length (Text-fig. 5B). The accentuation of these morphological parameters for the females does not constitute a true difference with the males. There is no acceleration of their morphology (McNamara 1986), only an hypermorphosis of ambulacra, correlated with the larger adult size.

However, for the other populations of *H.* (*L.*) *similis* and *H.* (*L.*) *leymeriei*, and in the limits of the samples under study, males and females have the same adult maximum size. The apparent hypermorphosis detected for some females *H.* (*L.*) *similis* cannot be recognized. Consequently, it is impossible to define the maximum size difference between males and females as a general sexual characteristic and, moreover, it is difficult to say if it is real or simply a sampling artefact.



TEXT-FIG. 6. Variation in gonopore diameter of *Mecaster cenomanensis* (Lower Cenomanian of Les Renardiéres, Charente-Maritime) according to the test sizes showing a rather large variability and no conspicuous genital dimorphism.

Comparison with Mecaster *species*. As mentioned above, several North African species of the hemiasterid genus *Mecaster* have been described as sexually dimorphic. Unfortunately, none of the authors have documented conspicuous genital differences associated with the morphological differences. In my own experience, an exhaustive morphological analysis of Cretaceous hemiasterids (Néraudeau 1990) has shown that sexual dimorphism can be detected biometrically for several globular species of North European hemiasterids, but never conspicuously for North African *Mecaster* species.

In most cases, the frequency distribution of gonopore diameter is almost unimodal for *Mecaster* species and the variations in gonopore diameter according to the size of individuals show a great variability (Néraudeau 1990; Text-fig. 6). That variability in gonopore diameter is too marked to permit the distinction of any sexual dimorphism and, therefore, *Mecaster* species would be characterized by tests showing no conspicuous sexual dimorphism.

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DIDIER NÉRAUDEAU
Centre des Sciences de la Terre, URA CNRS 157
Université de Bourgogne
6 bd Gabriel
21000 Dijon, France

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